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The effect of previously viewed velocities on motion extrapolation

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ABSTRACT

There is preliminary evidence for interference between subsequently encoded velocities. We explored this effect using a motion extrapolation paradigm. In Experiments 1 and 2, moving targets disappeared behind an occluder. Participants responded at the time when they thought the target should reappear. Participants responded as if the current velocity was faster after a previous trial with a fast velocity and vice versa. In Experiment 3 the targets reappeared either on-time, early or late. A greater proportion of early trials were reported 'correct' following a fast previous trial. These experiments indicate that blending occurs between successively encoded velocity representations.

1. Introduction

Many tasks require velocity information to be encoded and remembered in order to guide behaviour at a later time. It is thought that velocity information is processed in isolation from other visual dimensions such as spatial frequency, temporal frequency and direction (McKeefry, Burton, & Vakrou, 2007) and that perceptual velocity processing systems also store velocity information after stimulus offset (Pasternak & Greenlee, 2005). There is evidence for velocity storage from a number of lines of research. For example, in delayed discrimination paradigms participants can accurately discriminate the velocities of two successively presented moving gratings over delays of up to 30 s (Magnussen & Greenlee, 1992).

In motion extrapolation tasks (sometimes known as prediction-motion tasks), participants typically see a moving target which is then occluded and they attempt to judge when the target would reach a specified point on the occluded path (e.g., Rosenbaum, 1975). It has been suggested that motion extrapolation tasks are performed by using a timing strategy: participants may calculate the time needed for the target to reach a specified end point prior to occlusion and then respond after counting down this amount of time (Tresilian, 1995). However there is now extensive evidence that attentional tracking is used during motion extrapolation. Studies have shown that motion extrapolation is affected by spatial factors such as concurrent moving distractors (Lyon & Waag, 1995), the motion after-effect (Gilden, Blake, & Hurst, 1995) and geometrical illusions which alter perceived distance (DeLucia, Tresilian, & Meyer, 2000). Moreover, it has been found that people can keep their eyes roughly aligned with the position of occluded targets (Bennett & Barnes, 2006). Finally, people are able to extrapolate motion even when the target disappears and then reappears after an unpredictable period, rather than going behind an occluder. In these 'interruption paradigms' a countdown timing strategy cannot be used because it is impossible to calculate occlusion duration a priori (DeLucia & Liddell, 1998). So, although there is an ongoing debate[1] about the cognitive mechanisms underlying motion extrapolation (Benguigui, Broderick, & Ripoll, 2004; Pylyshyn, 2003), it seems that visuospatial attentive tracking mechanisms are involved. In this case, target velocity information encoded prior to occlusion is used to update the tracking mechanism at the correct rate (Bennett & Barnes, 2006; Wexler & Klam, 2001).

As well as delayed discrimination and motion extrapolation tasks, the control of smooth eye movements also relies on velocity memory (Barnes & Asselman, 1991). People cannot usually produce smooth eye movements in the absence of a moving target. Nevertheless, they can produce *anticipatory* smooth pursuit eye movements (ASPEMs), scaled according to the expected velocity of an upcoming target (Barnes, Goodbody, & Collins, 1995) or a target reappearing after occlusion (Bennett & Barnes, 2006). That is, the expectancy of a fast-moving target leads to a fast ASPEM while the expectancy of a slow target leads to a slow ASPEM. ASPEMs are produced even when fixation is maintained during previous exposure to moving targets (Barnes, Grealy, & Collins, 1997), indicating

[1] Although there are alternative theoretical frameworks for understanding time to contact judgments, notably those based on the tau hypothesis (e.g., Regan & Gray, 2000), these are typically used to explain perception of approaching objects. The cognitive strategies described above are thought to be associated with lateral motion extrapolation tasks (Tresilian, 1999).

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that they cannot be explained simply by the repetition of oculomotor responses. Rather, it is argued that stored representations of target velocity are used to scale ASPEM velocity (Barnes & Asselman, 1991).

The current research question concerns the interference between successively encoded velocities. This issue has been addressed in various contexts. Firstly, Magnussen and Greenlee (1992) reported that the presentation of a masker velocity during the delay period of their delayed discrimination task elevated discrimination thresholds. It was found that the greater the discrepancy between the velocity to be encoded and the masker velocity, the greater the threshold elevation. In a follow up study, McKeefry et al. (2007) found that altering the spatial and temporal frequency of the masker grating independently of its velocity did not produce the masking effect. Thus the effect can be attributed to interference between speed representations. Along similar lines, Kerzel (2001) found that the velocity of manual movement executed during the delay period of a visual velocity discrimination task interfered with remembered visual velocities. Storage of more than one velocity representation and interference between velocity representations has also been demonstrated with ASPEM data. It has been found that participants can learn sequences of velocities (Collins & Barnes, 2005) and that two simultaneously presented targets may be encoded (Poliakoff, Collins, & Barnes, 2004). In one study, participants fixated while watching two targets travelling horizontally rightward at different velocities (Poliakoff et al., 2004). Following a cue, one of the targets was presented again and participants were asked to track this target with their eyes. Their ASPEM velocity was scaled to the cued target velocity, indicating that both target velocities had been stored prior to the presentation of the cue. In a follow up experiment by Poliakoff, Collins, and Barnes (2005), the velocity of the *previous trial* was also found to systematically influence ASPEM velocity. The influence of the cued velocity from the previous trial was similar to that of the cued velocity in the current trial; faster previous velocities resulted in faster ASPEMs, and vice versa. Therefore ASPEMs appeared to have been guided by the target velocities presented in both the current and the previous trial (see also, Jarrett & Barnes, 2002), although only the latter predicted the upcoming target velocity. It seems that the two encoded velocities (that is, the cued velocity in the current and previous trial) may have *blended* to produce the ASPEM velocity.

Finally, the immediately preceding trial has also been observed to influence motion extrapolation. Lyon and Waag (1995) presented a target which travelled along a circular path before being occluded. An endpoint then appeared and participants judged whether the target would have passed this point or not. They found that the proportion of 'pass' responses increased when the velocity of the previous trial had been faster than the current trial and decreased when the previous velocity had been slower. Lyon and Waag (1995) suggested that the tracking process on the previous trial had converged with the current tracking process. Note that the incidental past history effects found by Lyon and Waag (1995) and Poliakoff et al. (2005), in which previous presentations (which were no longer task-relevant) interfered with current processing, are different from the interference effects observed by Magnussen and Greenlee (1992) and Kerzel (2001), in which a distractor interfered with the instructed retention of velocity between presentations.

Although there is some evidence for incidental past history effects in velocity processing from several paradigms (Jarrett & Barnes, 2002; Lyon & Waag, 1995; Poliakoff et al., 2005), there are a number of problems with the existing evidence. Poliakoff et al. (2005) and Jarrett and Barnes (2002) used the same presentation duration for all velocities, so target displacement was confounded with velocity; that is faster targets had longer trajectories and vice versa. It is therefore possible that target displacement and/or the maximum eye displacement on the previous trial might have produced the observed effects. Second, these past history effects were observed within complex cueing tasks, requiring participants to sometimes remember velocities between subsequent presentations. In other related work, the parameters from the previous trial have been shown to influence performance of eye and arm movements on the current trial, when they provide relevant information (de Lussanet, Smeets, & Brenner, 2001; Kowler, 1989). Therefore past history effects may *not* be seen when participants are never asked to remember velocities between trials. Third, only four different levels of velocity were presented in the ASPEM studies and participants would have become familiar with these, thus it is impossible to disentangle shorter and longer term encoding effects. In Lyon and Waag (1995), participants judged whether the target would have passed a certain point, so it is possible that previous velocities could have biased their tendency to respond one way or the other, rather than influenced motion extrapolation per se. Again displacement was not controlled in this experiment and only three levels of velocity were presented.

The current set of three experiments explored the influence of previously seen velocities on current velocity representations more directly by using a motion extrapolation task. The tasks used here were simpler than those of Poliakoff et al. (2005) and Jarrett and Barnes (2002), in that there was no requirement to retain velocity representations between trials. In Experiments 1 and 2 participants saw a moving target disappear behind a visible rectangular occluder and were asked to press a button at the exact time they thought the target should reappear. In Experiment 3, an interruption paradigm was used; the target disappeared rather then becoming occluded and reappeared either at the correct time, too early or too late. Participants judged whether the reappearance time was correct or incorrect. Note that the type of responses in all our experiments circumvent the complications associated with Lyon and Waag's judgment task where previous trials velocity could have biased the tendency to make a 'pass' or 'no pass' response. Finally, we presented 11 different levels of velocity, to increase uncertainty and to prevent over-familiarity with specific velocities.

In all three experiments, the influence of previous trial velocity (referred to as *prime trials*) on performance on the current trial (referred to as *probe trials*) was assessed. A past history effect was observed in all experiments, and the pattern of results suggests that there was blending between subsequently encoded velocities.

2. Experiment 1

In Experiment 1 participants viewed a rightward moving target which disappeared behind a rectangular occluder. They were instructed to press a button at the exact time that they thought the target would emerge on the right-hand side of the occluder. We examined the direction and size of the participants' error in response time (time of response minus would-be time of reappearance). To assess the influence of previous trials, probe trials travelling at 20°/s were systematically preceded by combinations of two prime trials. The primes were either faster (24 or 28°/s) or slower (12 or 16°/s) than the probe trial. The prime trials are referred to as the N-1 trial (immediately preceding the probe) and the N-2 trial (two trials before the probe). All combinations of faster and slower prime trials were presented. If error on the *probe trial* is systematically related to the velocity of the *prime trials*, this would demonstrate the existence of past history effects in velocity processing. Moreover, the *direction* of the effect allows us to gain

an insight into the interactions between velocity representations. For example, the blending of velocity representations account suggested by previous studies would be supported if *slower* prime trials are associated with *late* responses on the probe trials and if *faster* prime trials are associated with *early* responses.

Prime-prime-probe groups were separated by filler trials, with a different set of velocities. This reduced the predictability of the task, and prevented over-learning of the particular velocities (cf Ackerman, 1988) or sequences of velocities (Collins & Barnes, 2005). The range of velocities used here was comparable to those used in anticipatory eye movement tasks. For example, Poliakoff et al. (2005) used trials of 8°/s, 16°/s, 24°/s and 32°/s. As an influence of the previous trials was found in this study, a similar range of velocities was chosen for the current work. Although the target did not reappear on the right of the occluder in majority of trials, the target did reappear in a small number of the filler trials in order to maintain interest in the task (cf Gilden et al., 1995).

2.1. Method

2.1.1. Participants

Twenty-four participants aged 19–28 (9 male, 15 female, 5 left-handed, 19 right-handed) took part. The study had local ethics committee approval and participants gave written informed consent.

2.1.2. Apparatus

Participants sat at a table in a dimly lit room, with their head in a chin rest, approximately 75 cm from a 40 cm CRT monitor which subtended approximately 29.86° of their visual angle. Visual stimuli were presented using a ViSaGe Visual Stimulus Generator (Cambridge Research Systems). The target was a blue circle (RGB = 0, 0, 255) of 0.44° in diameter presented approximately at eye level, against a black background. The target always appeared 11.67° to the left of the screen centre and moved horizontally rightward[2]. This was achieved by presenting the target in a new position on every other frame (140 Hz). A grey occluder (RGB = 255, 123, 123) of 3.65° in height and 8.75°–11.67° in length, was presented on every trial with the leftmost edge being 1.46° to the left of the centre. The target path was aligned with the centre of the occluder. Participants rested their preferred hand on a button box and responded by pressing down with their index finger.

2.1.3. Design

The participants received the 20°/s probe target 32 times in total. It was preceded twice by every combination of prime trials: N-1 (12°/s, 16°/s, 24°/s, 28°/s) × N-2 (12°/s, 16°/s, 24°/s, 28°/s).

2.1.4. Procedure

Participants were instructed to press the button at the exact time that they thought the target should reappear from behind the occluder. Participants were not asked to fixate and no eye movement instructions were given. At the start of each trial, a 200 ms audio cue (approximately 300 Hz) was presented and the occluder appeared (Fig. 1). At the same time, the static target was presented for 200 ms to indicate the start point at the far left of the screen. The target was then blanked for 400 ms, before it reappeared moving horizontally rightward. The target was visible for 10.21° (between 340 and 1020 ms depending on the velocity), before disappearing behind the occluder. The occlusion duration varied from 292 to 1160 ms depending on the occluder size and the target velocity (the range was smaller for prime and probe trials; 312–972 ms).[3] The next trial began 6.3 s after the start of the previous trial. If no response was detected, a 200 ms higher frequency beep (approximately 450 Hz) was presented at the end of the trial to alert them.

Participants first completed a practice block of 22 trials (2 each of the 11 possible target velocities; 10–30°/s in 2°/s steps), in which the target reappeared on every trial (see Gilden et al., 1995). They then completed 192 trials, in which the target did not reappear for the majority. 96 trials were experimental prime-prime-probe trials: the probe velocity (20°/s) was presented 32 times, preceded twice by every combination of the prime velocities (64 presentations). All 16 different sets of prime-prime-probe trials were presented once before they were repeated. The remaining 96 trials were filler trials, with each of 6 velocities (10°/s, 14°/s, 18°/s, 22°/s, 26°/s, 30°/s) being presented 16 times. Between 2 and 5 filler trials were presented between every set of prime-prime-probe trials and the average velocity of a group of filler trials was always 16–24°/s. The target reappeared for 3 of the filler trials at each velocity although never on a trial immediately preceding a prime trial. Overall, the target reappeared on 12.5% of trials.

The 16 combinations of prime-prime-probe trials were presented in four blocks of 48–54 trials in a pseudorandom sequence separated by filler trials (see above). In order to minimise chance order effects that might be produced by the filler trials, another set of 4 blocks was produced by reversing the order of presentation of the sets of prime-prime-probe trials and the intervening blocks of filler trials. Half of the participants completed the original set of blocks and half the reversed blocks, with the order of block presentation being dictated by a Latin square. Each of the 8 possible block sets (forward/reverse × 4 possible block orders) was used 3 times.

2.1.5. Analysis

The judgement error was calculated for each trial (response time minus would-be time of reappearance), where a positive error reflects that the participant responded late (i.e. as if the target were travelling slower) and a negative error reflects an early response (i.e. as if the target were travelling faster). Trials were removed from analysis if there was no response recorded or the error was ±1000 ms from the would-be time of reappearance. This resulted in a loss of 10.3% of probe trials; the majority of these were due to the participant failing to respond or the equipment failing to detect a response. Then .65% of trials were removed due to being outliers (>2.5 standard deviations from the participant's mean error). Following the approach of Gilden et al. (1995), each participant's error in each condition was calculated with respect to their own mean error for probe (20°/s) trials. This compensated for the fact that some participants had a tendency to respond early or late across all trials. Note that the group mean probe trial error was 13.3 ms, with a range −183.0 to 254.4 ms. In addition, the subjective velocity was calculated for each of the filler trials (Gilden et al., 1995; Rosenbaum, 1975). That is, the apparent velocity of the target based upon the time at which the participant responded. For the ANOVA analysis, outliers more than 2.5 standard deviations from the mean for that condition were replaced by the next largest value plus 1 (4 values) and missing data points were replaced with the mean from that condition (3 values). When sphericity was violated, the Huynh–Feldt correction factor was used.

[2] It should be noted that the screen was flat, so the distance between target and participant is greater when the target is in peripheral locations. The values given are based on the degrees of visual angle at the center of the screen.

[3] Peterken, Brown, and Bowman (1991) found that extrapolation performance did not deteriorate within the range of occlusion durations used for prime and probe trials, and thus we would not expect the variability in this parameter to interfere with performance.

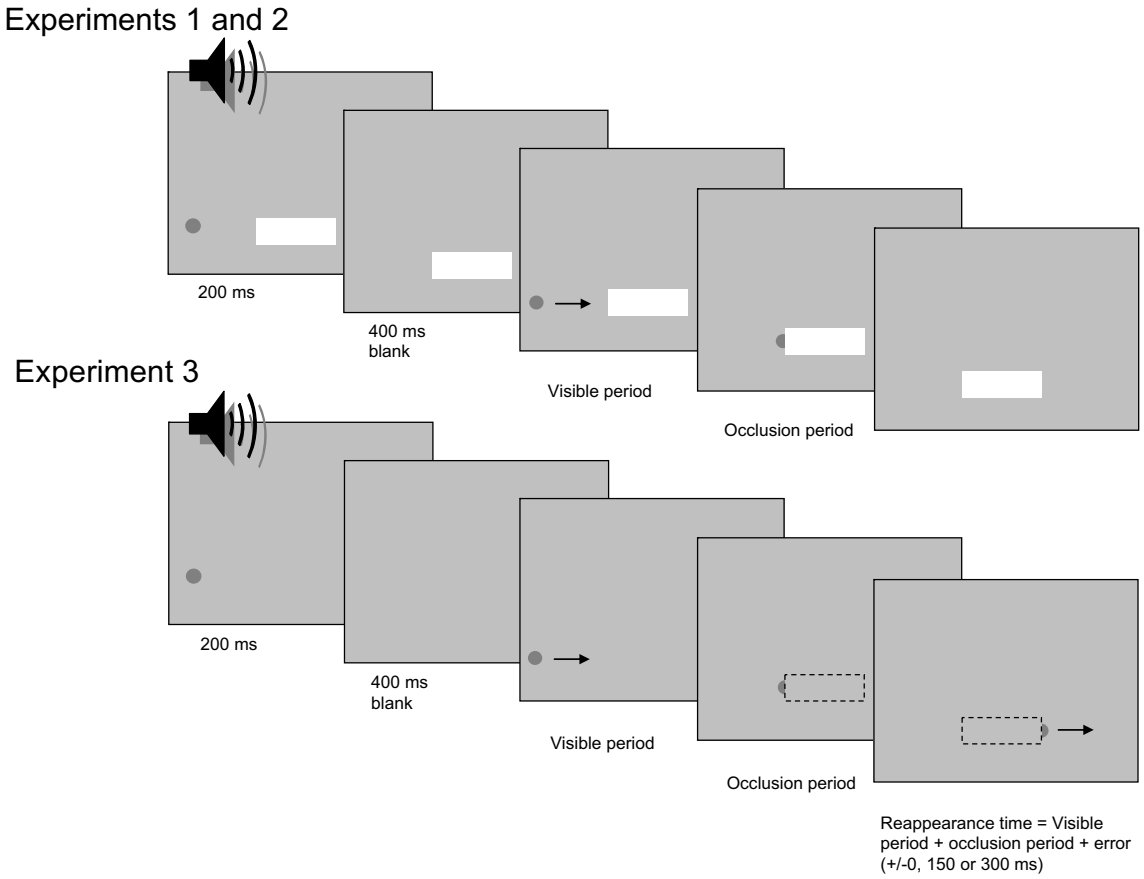

Fig. 1. The order of events in a single experimental trial. In Experiments 1 and 2, a static target and occluder appeared in conjunction with an audio cue. The target was then blanked and reappeared moving horizontally rightward, before disappearing behind the occluder. The participant pressed a button at the time they thought that the target should reappear. The screen was then blanked before the onset of the next trial. In Experiment 3, the target began to move in the same way before disappearing however the occluder was not visible. Reappearance occurred either at the correct time or with an error of ±150 or 300 ms, assuming a constant velocity during occlusion. Participants discriminated between correct and incorrect reappearances.

2.2. Results

To investigate the effect of prime trial velocity on probe trial response time, a 4×4 repeated measures ANOVA was carried out [N-1(12°/s, 16°/s, 24°/s, 28°/s) × N-2(12°/s, 16°/s, 24°/s, 28°/s)] on the probe mean error data. There was a main effect of N-1 velocity ($F(2.17, 49.95) = 5.170$, $p = .008$; Fig. 2A). When slower prime trials (12°/s and 16°/s) were presented in the N-1 position, then the probe trial error was positive (participants responded late). Conversely, when faster prime trials (24°/s and 28°/s) were presented in the N-1 position, the probe trial error was negative (participants responded early). There was a trend for slower N-2 velocities to produce late responses and faster N-2 to produce early responses, although this failed to reach significance ($F(1.46, 33.48) = 3.445$, $p = .057$, Fig. 2B). The interaction between N-1 and N-2 velocity was not significant ($F(3.39, 143.9) = 1.102$, $p = .365$). Linear contrasts revealed a significant positive relationship between N-1 velocity and probe trial error ($F(1,23) = 7.801$, $p = .01$) and a borderline significant positive relationship between N-2 velocity and probe trial error ($F(1,23) = 3.780$, $p = .064$).

The subjective velocities were analysed across the 10 prime and filler velocity levels (10°/s, 12°/s, 14°/s, 16°/s, 18°/s, 22°/s, 24°/s, 26°/s, 28°/s, 30°/s). The linear contrast for velocity was significant ($F(1,23) = 50.4$, $p < .0005$) and repeated contrasts revealed significant differences between each successive velocity for all pairings ($F(1,23) > 7.4$, $p < .013$) except between 18°/s and 22°/s, 26°/s and 28°/s and between 28°/s and 30°/s. The latter two reflect the more variable performances between participants at higher velocities (Fig. 2E).

2.3. Discussion

Analysis of subjective velocity revealed a strong linear relationship between subjective velocity and real velocity, indicating that participants were able to perform the motion extrapolation task. Importantly, the timing of responses on current trials was systematically related to the velocity of the previous (N-1) trials. If the immediately preceding trial was slow, this resulted in *later* responses on the current trial. Conversely, a faster immediately preceding trial led to an *earlier* response on the current trial. The results are consistent with the notion that the velocity representation used to guide responses on the current trial was a blend of the target velocity viewed on the current trial and the velocity of the previous trial. As outlined in the introduction, similar past history effects have also been demonstrated with anticipatory smooth pursuit eye movements (Jarrett & Barnes, 2002; Poliakoff et al., 2005). The N-2 trial had a similar, but statistically non-significant effect to the N-1 trial.

However, alternative explanations for the results of Experiment 1 must be considered. Because the occluder size was the same across velocities, slower velocities were occluded for longer. Thus, it could be that the *occlusion time* of the previous trial influenced responses on the current trial as well as, or instead of, the previous velocity. Indeed, interference between encoded temporal durations

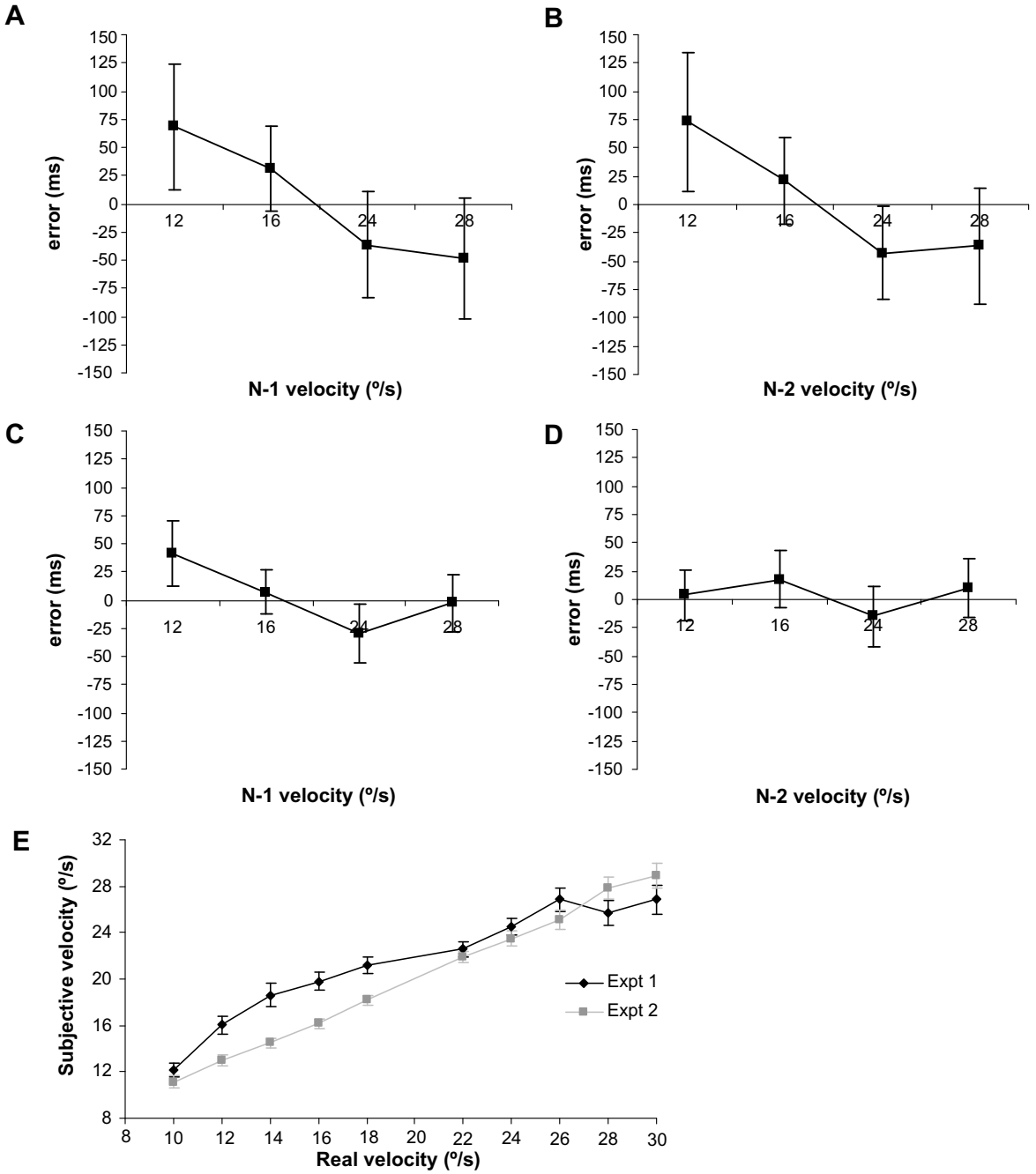

Fig. 2. (A–D) Mean (±SEM) error with respect to participant's mean error in the probe 20°/s trials in Experiments 1 and 2. (A) and (B) show data from Experiment 1, while (C) and (D) show data from Experiment 2. (A) and (C) show mean probe error for the four levels of N-1 velocity, while (B) and (D) show mean probe error for the four levels of N-2 velocity. A positive error reflects participants responding as if the target is slower and a negative error reflects participants responding as if the target is faster. (E) Mean (±SEM) subjective velocity (°/s) plotted against real velocity (°/s) for Experiments 1 and 2.

has been observed in tasks where the storage of more than one temporal representation is required (Jones & Wearden, 2004), while the order in which intervals are presented is known to alter their perceived duration (e.g., Allan & Gibbon, 1994). Although it is unlikely that responses were guided solely by temporal representations (DeLucia & Liddell, 1998, and see introduction) the regular relationship between velocity and occlusion duration may have encouraged participants to use a more time-based strategy and the previous occlusion duration could nevertheless have produced the past history effects observed in Experiment 1. Experiment 2 was carried out to address this issue.

3. Experiment 2

In Experiment 1, the occluder size was kept constant across all target velocities, and thus the occlusion time varied with target velocity. A fast trial was, on average, occluded for a shorter duration than a slow trial, and therefore the obtained results could have arisen from either previously represented velocities or occlusion durations. Experiment 2 was identical to Experiment 1, except that the occluder size was manipulated such that the target was occluded for 437 ms on every trial (the occlusion duration for a 20°/s target with an 8.75° occluder). Thus a past history effect in

Experiment 2 cannot be attributed to interference between representations of occlusion duration and would therefore provide stronger evidence for interference between subsequently encoded velocity representations.

3.1. Method

3.1.1. Participants

A different group of 24 participants took part in Experiment 2 (aged 21–30, 13 male, 11 female, 2 left-handed, 22 right-handed).

3.1.2. Design

The design, apparatus and procedure used in Experiment 2 were identical to that of Experiment 1, except the occluder size was manipulated such that the occlusion duration was always 437 ms. Thus, the occluder varied in size from 4.87° (for 10°/s trials) to 14.61° (for 30°/s trials).

3.1.3. Analysis

The approach was the same as for Experiment 1: probe trials were removed with errors ±1000 ms (9%) or >2.5 *SD* from the participants mean (1%). Error was again calculated with respect to each individuals probe mean (group mean = 51.87 ms; range −163.2 to 266.6 ms). In addition, 12 of data points were replaced by the next highest value plus 1 due to being > 2.5 *SD* from the condition mean. 3 missing data points were replaced with the mean from that condition for ANOVA.

3.2. Results

There was a marginally significant main effect of N-1 velocity ($F(1.88, 43.26) = 3.313$, $p = .049$; Fig. 2C). However, the N-2 main effect ($F(3, 69) = 2.358$ $p = .079$; Fig. 2D) and the interaction ($F(6.93, 159.34) = 1.725$, $p = .108$) were not significant. As in Experiment 1, slower N-1 trials resulted in late responding on probe trials and faster N-1 trials resulted in early responding on probe trials. However, linear contrasts did not show a significant relationship between N-1 velocity and probe error ($F(1, 23) = 2.772$ $p = .109$) or between N-2 velocity and probe error ($F(1, 23) = .091$ $p = .766$).

The subjective velocities were again analysed across the 10 velocity levels other than 20°/s (10°/s, 12°/s, 14°/s, 16°/s, 18°/s, 22°/s, 24°/s, 26°/s, 28°/s, 30°/s). The linear contrast was significant ($F(1, 23) = 165.777$ $p = <.005$) and repeated contrasts revealed a significant difference between every level ($F(1, 23) > 6.965$ $p < .01$; Fig. 2).

3.2.1. Comparison of Experiments 1 and 2

To explore differences between Experiments 1 and 2, a 3 way ANOVA was conducted with N-1 and N-2 velocity as within-participant factors and Experiment as a between-participants factor. There was a main effect of N-1 velocity ($F(2.06, 94.94) = 7.868$, $p < .001$) and N-2 velocity ($F(1.57, 72.02) = 3.96$, $p = .03$) on probe error. However, there was no significant main effect of Experiment ($F(1, 46) = .713$, $p = .403$), nor were there significant N-1 × N-2 ($F(6.89, 319.69) = 1.378$, $p = .215$) or N-1 × Experiment ($F(2.06, 94.94) = 1.359$, $p = .262$) interactions. The N-2 × Experiment interaction, however, approached significance ($F(1.57, 72.02) = 2.774$, $p = .084$).

3.3. Discussion

In Experiment 2, the effect of N-1 trial velocity was similar to that found in Experiment 1. Again the presentation of slower N-1 trials resulted in late responses on the current trial and fast N-1 trials resulted in early responses on the current trial. This supports the idea that velocity representations blend across subsequent trials and influence motion extrapolation performance. Given that occlusion duration was controlled in Experiment 2, this result cannot be due to interactions between representations of occlusion duration. Although it appeared that the N-1 effect was smaller in Experiment 2 than Experiment 1, there was no Experiment x N-1 interaction. However, the Experiment x N-2 interaction approached significance reflecting the fact that there was a borderline significant N-2 effect in Experiment 1 but not in Experiment 2.

There are several possible explanations for the trend towards a smaller effect size in Experiment 2. The first is that representations of occlusion duration were partially responsible for the past history in Experiment 1, so the elimination of this confound reduced the influence of the previous trial. Second, ceiling effects may have attenuated the influence of the previous trial in Experiment 2. This is suggested by the stronger relationship between subjective and real velocity than in Experiment 1. Participants may have implicitly learned the constant occlusion duration (e.g., Johnstone & Shanks, 2001), or to use occluder size as an indicator of reappearance time (cf Jarrett & Barnes, 2002). Third, another consequence of controlling occlusion duration was that in slower trials the end of the occluder was further to the left than for faster trials. Thus, if participants tended to respond when the target was at a similar *location* to the reappearance point on the previous trial, the velocity blending effect would be counteracted. Finally, the variation in occluder size between trials in Experiment 2 may have made the difference between successive trials more apparent, leading to greater refreshing of velocity processing mechanisms, and thereby reduced the influence of the previous trial. In support of this, Poliakoff et al. (2005) found that blending was modulated by attention. This effect could be interpreted within the framework of event files (see Hommel, 2004 for review), with blending resulting from the partial activation of an *event file* associated with the previous trial. Thus, the greater discrepancy in visual features between trials in Experiment 2 may have reduced the activation of the event file associated with the previous trial, and therefore reduced the size of the blending effect.

Despite the reduction of effect size in Experiment 2, the results are consistent with those of Experiment 1, but cannot be attributed to blending between successive representations of occlusion duration, as the occlusion duration was always identical. However, another potential confound in Experiment 2 must be considered. Although occlusion duration was controlled, the overall duration from trial onset to would-be reappearance (and response) was proportional to target velocity. The time of response could, therefore, have carried over from the previous trial and produced the observed past history effect. In summary, the findings of Experiment 2 are weakened by the possibility that participants may have adopted an inappropriate strategy as a result of the constant occlusion duration, and the fact that the past history effect could be explained by a general carry over of the response time from the previous trial. Experiment 3 was carried out to address these issues.

4. Experiment 3

The aim of Experiment 3 was to replicate the findings of Experiments 1 and 2 using an interruption paradigm (e.g., DeLucia & Liddell, 1998; Lyon & Waag, 1995). The target was seen to move rightward before disappearing smoothly behind an invisible occluder, which was the same colour as the background, so the screen was blank during occlusion (Fig. 1). Occlusion duration and the position of reappearance were always unpredictable, thus preventing any a priori knowledge of when or where reappearance would occur. On some trials, the target reappeared at the correct time,

assuming it had continued at a constant velocity across the occlusion interval. In other trials, the target reappeared at the correct velocity but 150 or 300 ms too early or too late. Participants discriminated correct from incorrect reappearance by means of a non-speeded button press response.

There were three advantages to this approach. First, the increased uncertainty about the point at which the target will reappear should have discouraged the participants from adopting an inappropriate strategy. In Experiment 1, the regular occluder size may have encouraged participants to learn and use the relationship between velocity and occlusion duration, whereas in Experiment 2, participants could learn to respond 437 ms after the target had been occluded, either due to feedback on the reappearance trials or through incidental encoding of trial parameters. In Experiment 3, there was no possibility of using cues other than the targets velocity to guide judgments. Second, the response was *unspeeded*; participants were not attempting to press a button at an exact time. As mentioned above, while the occlusion duration was controlled in Experiment 2, the timing of the responses, with respect to trial onset, was still proportional to target velocity. The past history effect could therefore be explained by the carry over of the timing of the response (with respect to the trial onset) from the previous trial. With an unspeeded discrimination response in Experiment 3 the timing of response initiation in the previous trial cannot account for any past history effect.

Third, the use of an interruption paradigm further ensured that participants were not using a countdown timing strategy (Tresilian, 1995). In an interruption paradigm there is no visible occluder or reappearance point, so it is impossible to calculate the occlusion duration in advance and a timing strategy is not viable (DeLucia & Liddell, 1998). Therefore in Experiment 3 any possible alternative explanations for the blending effect involving representations of occlusion duration are implausible.

To assess the influence of previously seen velocities, probe trials of 20°/s were used again. In order to increase the number of repeats in each condition, only two levels of N-1 velocity, 14°/s and 26°/s were used and because the previously observed N-2 effects were marginal, the N-2 velocity was kept equivalent between N-1 conditions, but not analysed. If subsequently encoded velocity representations blend (as might be expected from the results of Experiments 1 and 2), then *early* probes would be more likely to be erroneously reported as correct after a *fast* prime. Conversely, *late* probes would be more likely to be judged as correct after a *slow* prime.

Note that the use of two alternative forced choice method required measures to avoid the issue of *response type* carrying over from the previous trials. First, we used a correct/incorrect judgment rather than pass/no pass judgement to avoid associations between previous trial velocity and a particular response type (e.g., a fast trial leading to a 'pass' response). Second, the prime trial target always reappeared at the correct time. This ensured that prime trials only differed from probe trials in terms of velocity, and thus past history effects could not be explained by the reappearance error or response on the previous trial.

4.1. Method

4.1.1. Participants

Twenty-four participants (aged 17–40, 4 left-handed, 20 right-handed, 7 male, 17 female) were involved. All participants had normal or corrected to normal vision.

4.1.2. Apparatus

The experimental setup was the same as in Experiments 1 and 2. The blue target always appeared 13.12° to the left of the screen centre and moved horizontally rightward. However, for this experiment the occluder was the same colour as the background and thus invisible (Fig. 1).

4.1.3. Design

There were ten conditions [Prime trial (14°/s, 26°/s) × Reappearance error (−300, −150, 0, 150 or 300 ms)].

4.1.4. Procedure

Participants pressed one of two buttons depending on whether they judged reappearance to have occurred at the correct or incorrect time, assuming a constant velocity during the occlusion period. The appearance of the target was identical to Experiment 1 (with audio cue and blanking) and again no eye movement instructions were given. On all trials, the target trajectory was 26.25°, presented at the centre of the screen. The first visible period was always 5.95° in length. This was followed by an occlusion period. The length of the occlusion period ranged from 5.77 to 11.72°. This corresponds to a minimum and maximum hidden duration of 192 and 1172 ms, depending on velocity. Reappearance error was produced by adding or subtracting 0, 150 or 300 ms from the occlusion duration, without altering the length of the occluded trajectory. The interval between reappearance time of prime trials and the start of the probe trial was always 3400 ms. This value was randomized between 3400 and 4400 ms in all other cases.

Each participant was first presented with a practice block consisting of 20 trials, 2 at each of the following velocities: 10°/s, 12°/s, 14°/s, 16°/s, 18°/s, 22°/s, 24°/s, 26°/s, 28°/s and 30°/s. The 5 levels of reappearance error each occurred 4 times during practice. The other parameters of the hidden period were randomized during practice.

Participants then completed 336 trials, 160 of which were experimental trials, consisting of prime-probe pairs. There were 80 probes, all of which travelled at a velocity of 20°/s. Half the probes were preceded by 14°/s primes and half by 26°/s primes. Primes always reappeared at the correct time. Probes were presented 8 times at each of the 5 levels of reappearance error. On probe trials the visible portion always lasted 300 ms. Each probe trial had one of four levels of occluded distance, 6.77°, 7.77°, 9.74° or 10.73° (Presented in a pseudorandom order, counterbalanced across reappearance error, prime velocity, and prime trial occlusion duration). On probe trials that appeared at the correct time, this corresponded to hidden durations of 338, 388, 487 and 536 ms. On prime trials the first visible period was 425 ms when velocity was 14°/s and 229 ms when velocity was 26°/s. The same 4 occluder sizes were used in the prime trials as the probe trials. In each prime probe pair the distance travelled by the occluded target was identical.

The remaining 176 trials were filler trials. The N-2 filler trials (before prime trials) always had a velocity of 16°/s, 18°/s, 22°/s or 24°/s and a reappearance error of ±150 ms. The remaining fillers trials had velocities of 10°/s, 12°/s, 28°/s and 30°/s (each presented 15 times in total), with each level of reappearance error occurring three times for each velocity, and velocities of 16°/s 18°/s 22°/s and 24°/s with reappearance errors of 0 or ±300 ms. The number of filler trials separating prime probe pairs was either 2 or 3. The average velocity of all filler trials between prime-probe pairs always ranged between 16°/s and 24°/s and the average reappearance error of each group of fillers was controlled so as to range between 150 and −150 ms. Other occlusion parameters were randomized on a trial by trial basis in the filler trials.

4.2. Results

The proportion of probe trials judged to have reappeared at the correct time was significantly affected by reappearance error ($F(2.99, 68.86) = 25.862$, $p < .001$). As can be seen in Fig. 3A, this

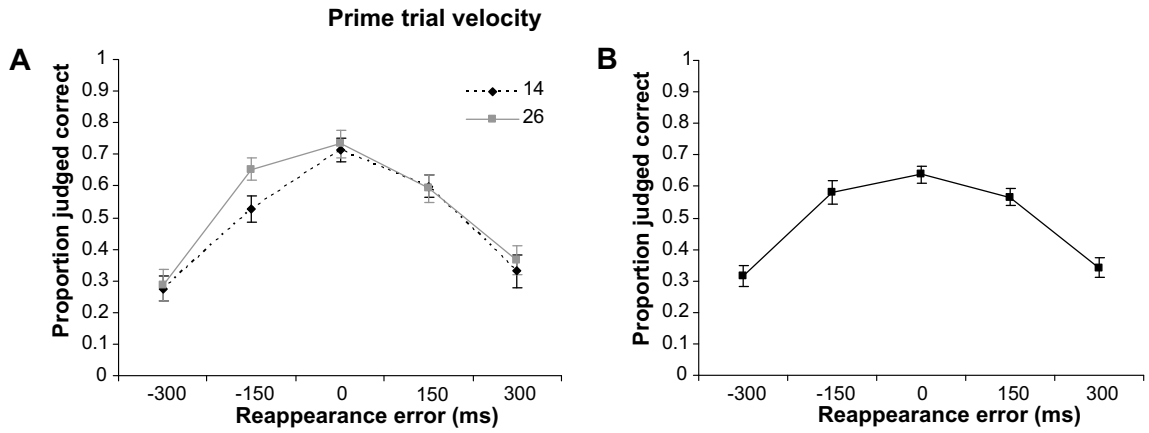

Fig. 3. (A) The proportion of 20°/s probe trials judged correct as a function of reappearance error and prime trial velocity. Error bars = ±1 SEM. (B) The proportion of filler trials judged correct as a function of reappearance error. Error bars = ±1 SEM.

was due to the highest proportion of 'correct' judgments when the target reappeared at the correct time (confirmed by a highly significant quadratic component; $F(1,23) = 80.073$, $p < .001$). There was also a significant effect of prime trial velocity ($F(1,23) = 4.948$, $p = .036$). There was no interaction between prime velocity and reappearance error ($F(3.41,78.51) = 1.681$, $p = .18$). However, paired samples t tests revealed a significant effect of prime trial velocity on the proportion of early probes targets judged to be correct. These trials were more likely to be judged correct if the prime trial was 26°/s ($t(23) = 3.164$, $p = .004$). There were no significant effects of prime velocity at the other reappearance levels ($t(23) < .993$, $p > .331$).

Analysis of judgments on the prime trials revealed that there was no significant difference between the proportion of fast ($M = .67$, $SD = .15$) and slow primes judged to have reappeared at the correct time ($M = .69$, $SD = .11$; $t(23) = .502$, $p = .62$). This indicates that the difference in responses to the probe trials following the fast and slow primes is unlikely to have been caused by a greater proportion one response type (correct/incorrect) on the previous trial. When the filler trials were analyzed there was again a significant effect of reappearance error ($F(2.76,63.58) = 24.208$, $p < .001$). As shown in Fig. 3B, this was due to accurate responses, with the highest proportion judged correct for correct trials (quadratic, $F(1,23) = 95.994$, $p < .001$).

4.3. Discussion

In Experiment 3 an interruption paradigm was used and a past history effect was again evident. When the probe target reappeared 150 ms early, participants were more likely to report a correct reappearance following a faster target on the previous trial. This is consistent with the idea that the fast velocity representation from the prime trial blended with the velocity representation used on the probe trial. When the probes reappeared 300 ms too early or late there was no effect of the prime trial. This presumably reflects a ceiling effect, whereby reappearance error exceeded any shifts in subjective velocity caused by the previous trial. There was also no effect when the probe reappeared 150 ms late. The velocity blending account, supported by the results of Experiment 1 and 2, would have predicted an increased proportion of correct responses after a slow prime trial in this condition. A potential explanation for this is that people overestimate short occlusion durations (Benguigui et al., 2004), which may have masked the influence of the previous trial in Experiment 3.

The presence of a comparable past history effect in Experiment 3 adds to the data from Experiments 1 and 2 in a number of ways. The past history effects in Experiment 1 may have been the result of interactions between subsequently encoded representations of occlusion duration, while the past history effects in Experiment 2 may have been due to a carry over of response time with respect to the start of the trial. In Experiment 3 both these possibilities are unlikely. Participants must have used velocity information encoded prior to occlusion to track the occluded target, as the temporal and spatial characteristics of the occlusion period were not available before the target actually reappeared. Meanwhile, the use of an unspeeded forced choice response rather than a timed response eliminates the possibility that the effect of an interest could be an artifact of the timing of the response on the previous trial.

5. General discussion

In both Experiments 1 and 2, participants responded as if current trials were slower than they really were after the presentation of slow trials, and faster after the presentation of fast trials. This pattern of interference is consistent with the idea that successive velocity representations blend to some extent. Furthermore, this effect cannot be entirely attributed to blending between representations of occlusion duration, as it was still present in Experiment 2 where this parameter was controlled. In Experiment 3, an interruption paradigm was used and results were again consistent with the velocity blending account. Participants tended to judge targets which reappeared too early as correct following a fast previous trial. This result cannot be attributed to past history effects on the timing of the response. The results of all three experiments are consistent with the idea that the velocity of a previously viewed moving object can influence current motion extrapolation performance.

As outlined in the introduction, previous studies have found comparable results. For example, ASPEM velocity is influenced by both relevant velocity information and previously viewed velocities (Jarrett & Barnes, 2002; Poliakoff et al., 2005). Similarly, Lyon and Waag (1995) found that judgments about whether an occluded target had passed an end point were influenced by the velocity in the previous trial.[4] In the current study, we have been able to rule out a number of alternative explanations for these observations. First, we have demonstrated a past history effect for velocity in a simpler task that did not require the participant to link numeric

[4] Note that in their experiment 2 Lyon and Waag (1995) used a slower range of velocities then was used in the current research (4, 6 and 8°/s as opposed to 10–30°/s) and extrapolation was carried out over a longer occlusion duration (the maximum was 7 s as opposed to 972 ms). Finally in this experiment, the targets travelled along a circular trajectory prior to disappearance, whereas the target travelled horizontally before disappearing behind an occluder in ours.

cues to velocities (Jarrett & Barnes, 2002), nor to remember simultaneously presented velocities (Poliakoff et al., 2005). Second, the results cannot be explained by response bias: the findings of Lyon and Waag (1995) could have been due to participants being more likely to choose the pass response following a faster N-1 velocity, rather than a change in velocity representation per se. Third, a large number of different velocities were presented within our experiments, which means that participants are unlikely to have learned our velocity set. Our results also parallel the interference in motion representation described in the introduction (Magnussen & Greenlee, 1992; McKeefry et al., 2007) and also the reduction in subjective velocity following motion adaptation (e.g., Hammett, Thompson, & Bedingham, 2000), which again highlights the role of previous input on current velocity processing.

At a practical level, our results suggest that it is essential to control for the velocity of previous trials in motion extrapolation experiments, as this may inadvertently influence errors in velocity judgment which may be attributed to other factors. Randomization of a velocity set may be insufficient because chance differences in previous velocities between conditions may confound the effect of interest. At a theoretical level, our results provide a starting point to consider the storage and representation of velocity. There are many open questions about our observed effect, which can be explored in future research. For example, what is the time course of the effect? This could be explored by manipulating the interval between trials and thus the decay of the representation of the previous trial. This would provide a measure of the duration of velocity memory. This approach may also provide a method of investigating a difficult issue in the literature; it is unclear to what extent a common velocity storage mechanism underlies performance of different tasks such as motion extrapolation and velocity discrimination.

Another issue that could be explored in future is the interaction between the blending effect and other cognitive influences. One possibility is that trials have to be perceived as repetitions of the same event in order for velocity representations to blend. That is, blending of velocity information may only occur within certain 'event files' (Hommel, 2004). The trend for a reduced effect size in Experiment 2 compared to Experiment 1 may reflect this. As discussed previously, Poliakoff et al. (2005) found a past history effect from attended, but not unattended, targets which indicates that blending only occurs between velocity representations which are cognitively grouped together in some way. It is also likely the semantic representation of the target could influence blending effects. Indeed, it has been found that people remembered the disappearance point of a moving triangle as being further along the trajectory of motion when the target was labeled a 'rocket' rather than a 'steeple' (Reed & Vinson, 1996). Other studies have found that static images which imply movement activate visual brain regions involved in the perception of real movement, such as areas MT (medial temporal) and MST (medial superior temporal, Kourtzi & Kanwisher, 2000). As these areas are likely to be involved in the encoding and retention velocity information (Born & Bradley, 2005; Greenlee, Lang, Mergner, & Seeger, 1995), we predict that the blending effect may also be modulated by top down inputs.

What mechanism underlies the past history effects found here? There are several possibilities that are not necessarily mutually exclusive. The results are consistent with the hypotheses outlined in the introduction: motion extrapolation relies on stored velocity representations for accurate tracking of the occluded target, and velocity representations from the previous trial blend with those used on the current trial. A similar account of interference between successive motion representations (beyond the early stages of processing) is proposed by McKeefry et al. (2007) to account for the masking effects observed in memory tasks (described in the Introduction). Blending between successive representations within the velocity store would lead to the pattern of results seen in both eye movement experiments and the current research. A related possibility is that the velocity of the previous trial could influence the operation of the visuospatial attentional tracking mechanism which is also necessary for motion extrapolation. Indeed, Lyon and Waag (1995) interpreted their blending effect in terms of convergence of the attentional spotlight velocity with that of the previous trial.

The current results could also be explained by a carry over of smooth pursuit eye movement velocity from the previous trial. It is known that eye movements are not necessary to encode velocity (Barnes et al., 1997) and that accurate judgements in motion extrapolation tasks can be made under conditions of fixation (Peterken et al., 1991). Nevertheless, it is possible that smooth eye movements play a role in motion extrapolation when they are permitted (Bennett & Barnes, 2006; Wexler & Klam, 2001). This is suggested by the reduction or absence of the motion-related representational momentum effect (the mislocalisation of the final position of a moving target further along its trajectory) when participants fixate (Kerzel, 2006). Note that the past history effects observed by Poliakoff et al. (2005) and Jarrett and Barnes (2002) could have been due to previously executed smooth eye movements. To explore the possibility that blending comes from the carry over of eye movement velocity, it will be necessary to analyse the effect during fixation in future experiments. However, the distinction between smooth attentional tracking and smooth pursuit eye movements may not be clear-cut. Just as mechanisms controlling saccadic eye movements overlap with those controlling abrupt shifts of attention. (e.g., Eimer, Van Velzen, Gherri, & Press, 2007), there is evidence for overlap between brain areas used for attentive tracking and gaze tracking (Ohlendorf, Kimmig, Glauche, & Haller, 2007).

Several studies have investigated the neural systems involved in tracking visible and occluded targets. For example, in one fMRI study the right MT/MST complex and bilateral intraparietal sulci (IPS) regions were found to be activated by viewing both visible and occluded movement (Olson, Gatenby, Leung, Skudlarski, & Gore, 2004). In another fMRI study by Lencer et al. (2004), tracking visible targets and targets which had disappeared for 1 s mid-trajectory were found to activate an overlapping network of areas. Activations in bilateral anterior-ventral IPS, FEFs and the right posterior IPS increased following target disappearance, while activations in V3a and MT remained equivalent. This suggests that extraretinal input enhances activity in tracking networks when targets disappear. Moreover, there were additional activations in the Dorsolateral Pre-frontal cortex (DLPFC) and right pre-supplementary eye fields when the target disappeared, which may reflect the increased reliance on velocity memory after target disappearance.

Microelectrode recording studies have also reported activity in some of these areas while monkeys tracked 'imaginary' targets (Assad & Maunsell, 1995; Ilg & Thier, 2003) and velocity sensitive neurons in the frontal eye fields (FEFs) have been found to fire during occlusion periods (Barborica & Ferrera, 2003). Meanwhile, lesions to the MT/MST complex impair performance on velocity discrimination tasks in monkeys (Pasternak & Merigan, 1994) and humans (Greenlee et al., 1995), while TMS stimulation applied to MT between presentations has been found to eliminate the priming effect of previous trials on direction sensitivity (Campana, Cowey, & Walsh, 2006). Given these findings, one possibility is that MT/MST along with frontal regions such as the DLPFC and the FEFs store velocity information, while the IPS exploits this information to update representations of target location at the correct rate during occlusion. The blending effect described above could be due to interference between processing of successive trials within any region of this fronto-parietal network.

6. Conclusions

The results of this series of experiments demonstrate that the velocity of previous trials can influence current velocity judgments. The direction of this past history effect suggests that subsequently encoded velocity representations partially blend together. Further research will be required to elucidate the level at which this past history effect manifests, i.e. whether the previous presentations influence attentional tracking, velocity storage or eye movements.

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References

Ackerman, P. L. (1988). Determinants of individual differences during skill Acquisition: Cognitive abilities and information processing. *Journal of Experimental Psychology: General, 117*(3), 288–318.

Allan, L. G., & Gibbon, J. (1994). A new temporal illusion or the toe once again. *Perception & Psychophysics, 55*(2), 227–229.

Assad, J. A., & Maunsell, J. H. R. (1995). Neuronal correlates of inferred motion in primate posterior parietal cortex. *Nature, 373*(6514), 518–521.

Barborica, A., & Ferrera, V. P. (2003). Estimating invisible target speed from neuronal activity in monkey frontal eye field. *Nature Neuroscience, 6*(1), 66–74.

Barnes, G. R., & Asselman, P. (1991). The mechanism of prediction in human smooth pursuit eye-movements. *Journal of Physiology-London, 439*, 439–461.

Barnes, G. R., Goodbody, S., & Collins, S. (1995). Volitional control of anticipatory ocular pursuit responses under stabilized image conditions in humans. *Experimental Brain Research, 106*(2), 301–317.

Barnes, G. R., Grealy, M., & Collins, S. (1997). Volitional control of anticipatory ocular smooth pursuit after viewing, but not pursuing, a moving target: evidence for a re-afferent velocity store. *Experimental Brain Research, 116*(3), 445–455.

Benguigui, N., Broderick, M., & Ripoll, H. (2004). Age differences in estimating arrival-time. *Neuroscience Letters, 369*(3), 197–202.

Bennett, S. J., & Barnes, G. R. (2006). Combined smooth and saccadic ocular pursuit during the transient occlusion of a moving visual object. *Experimental Brain Research, 168*(3), 313–321.

Born, R. T., & Bradley, D. C. (2005). Structure and function of visual area MT. *Annual Review of Neuroscience, 28*, 157–189.

Campana, G., Cowey, A., & Walsh, V. (2006). Visual area V5/MT remembers "what" but not "where". *Cerebral Cortex, 16*(12), 1766–1770.

Collins, C. J. S., & Barnes, G. R. (2005). Scaling of smooth anticipatory eye velocity in response to sequences of discrete target movements in humans. *Experimental Brain Research, 167*(3), 404–413.

de Lussanet, M. H. E., Smeets, J. B. J., & Brenner, E. (2001). The effect of expectations on hitting moving targets: Influence of the preceding target's speed. *Experimental Brain Research, 137*(2), 246–248.

DeLucia, P. R., & Liddell, G. W. (1998). Cognitive motion extrapolation and cognitive clocking in prediction motion tasks. *Journal of Experimental Psychology: Human Perception and Performance, 24*(3), 901–914.

DeLucia, P. R., Tresilian, J. R., & Meyer, L. E. (2000). Geometrical illusions can affect time-to-contact estimation and mimed prehension. *Journal of Experimental Psychology: Human Perception and Performance, 26*(2), 552–567.

Eimer, M., Van Velzen, J., Gherri, E., & Press, C. (2007). ERP correlates of shared control mechanisms involved in saccade preparation and in covert attention. *Brain Research, 1135*(1), 154–166.

Gilden, D., Blake, R., & Hurst, G. (1995). Neural adaptation of imaginary visual-motion. *Cognitive Psychology, 28*(1), 1–16.

Greenlee, M. W., Lang, H. J., Mergner, T., & Seeger, W. (1995). Visual short-term-memory of stimulus velocity in patients with unilateral posterior brain-damage. *Journal of Neuroscience, 15*(3), 2287–2300.

Hammett, S. T., Thompson, P. G., & Bedingham, S. (2000). The dynamics of velocity adaptation in human vision. *Current Biology, 10*(18), 1123–1126.

Hommel, B. (2004). Event files: Feature binding in and across perception and action. *Trends in Cognitive Sciences, 8*(11), 494–500.

Ilg, U. J., & Thier, P. (2003). Visual tracking neurons in primate area MST are activated by smooth-pursuit eye movements of an "imaginary" target. *Journal of Neurophysiology, 90*(3), 1489–1502.

Jarrett, C. B., & Barnes, G. R. (2002). Volitional scaling of anticipatory ocular pursuit velocity using precues. *Cognitive Brain Research, 14*(3), 383–388.

Johnstone, T., & Shanks, D. R. (2001). Abstractionist and processing accounts of implicit learning. *Cognitive Psychology, 42*(1), 61–112.

Jones, L. A., & Wearden, J. H. (2004). Double standards: Memory loading in temporal reference memory. *Quarterly Journal of Experimental Psychology Section B—Comparative and Physiological Psychology, 57*(1), 55–77.

Kerzel, D. (2001). Visual short-term memory is influenced by haptic perception. *Journal of Experimental Psychology-Learning Memory and Cognition, 27*(4), 1101–1109.

Kerzel, D. (2006). Why eye movements and perceptual factors have to be controlled in studies on "representational momentum". *Psychonomic Bulletin & Review, 13*(1), 166–173.

Kourtzi, Z., & Kanwisher, N. (2000). Activation in human MT/MST by static images with implied motion. *Journal of Cognitive Neuroscience, 12*(1), 48–55.

Kowler, E. (1989). Cognitive expectations, not habits, control anticipatory smooth oculomotor pursuit. *Vision Research, 29*(9), 1049–1057.

Lencer, R., Nagel, M., Sprenger, A., Zapf, S., Erdmann, C., Heide, W., et al. (2004). Cortical mechanisms of smooth pursuit eye movements with target blanking: An fMRI study. *European Journal of Neuroscience, 19*(5), 1430–1436.

Lyon, D. R., & Waag, W. L. (1995). Time-course of visual extrapolation accuracy. *Acta Psychologica, 89*(3), 239–260.

Magnussen, S., & Greenlee, M. W. (1992). Retention and disruption of motion information in visual short-term-memory. *Journal of Experimental Psychology—Learning Memory and Cognition, 18*(1), 151–156.

McKeefry, D. J., Burton, M. P., & Vakrou, C. (2007). Speed selectivity in visual short term memory for motion. *Vision Research, 47*(18), 2418–2425.

Ohlendorf, S., Kimmig, H., Glauche, V., & Haller, S. (2007). Gaze pursuit, 'attention pursuit' and their effects on cortical activations. *European Journal of Neuroscience, 26*(7), 2096–2108.

Olson, I. R., Gatenby, J. C., Leung, H. C., Skudlarski, P., & Gore, J. C. (2004). Neuronal representation of occluded objects in the human brain. *Neuropsychologia, 42*(1), 95–104.

Pasternak, T., & Greenlee, M. W. (2005). Working memory in primate sensory systems. *Nature Reviews Neuroscience, 6*(2), 97–107.

Pasternak, T., & Merigan, W. H. (1994). Motion perception following lesions of the superior temporal sulcus in the monkey. *Cerebral Cortex, 4*(3), 247–259.

Peterken, C., Brown, B., & Bowman, K. (1991). Predicting the future position of a moving target. *Perception, 20*(1), 5–16.

Poliakoff, E., Collins, C. J. S., & Barnes, G. R. (2004). Target selection for predictive smooth pursuit eye movements. *Experimental Brain Research, 155*(1), 129–133.

Poliakoff, E., Collins, C. J. S., & Barnes, G. R. (2005). Attention and selection for predictive smooth pursuit eye movements. *Cognitive Brain Research, 25*(3), 688–700.

Pylyshyn, Z. W. (2003). Mental imagery: In search of a theory. *Behavioral and Brain Sciences, 25*(2), 157–238.

Reed, C. L., & Vinson, N. G. (1996). Conceptual effects on representational momentum. *Journal of Experimental Psychology—Human Perception and Performance, 22*(4), 839–850.

Regan, D., & Gray, R. (2000). Visually guided collision avoidance and collision achievement. *Trends in Cognitive Sciences, 4*(3), 99–107.

Rosenbaum, D. A. (1975). Perception and extrapolation of velocity and acceleration. *Journal of Experimental Psychology—Human Perception and Performance, 1*(4), 395–403.

Tresilian, J. R. (1995). Perceptual and cognitive-processes in time-to-contact estimation—Analysis of prediction-motion and relative judgment tasks. *Perception & Psychophysics, 57*(2), 231–245.

Tresilian, J. R. (1999). Visually timed action: time-out for 'tau'? *Trends in Cognitive Sciences, 3*(8), 301–310.

Wexler, M., & Klam, F. (2001). Movement prediction and movement production. *Journal of Experimental Psychology—Human Perception and Performance, 27*(1), 48–64.